On the Origin of Insects. By Sir John Lubbock, Bart.

[Read November 2, 1871.]

The metamorphoses of this group have always seemed to me one of the greatest difficulties of the Darwinian theory. In most cases the development of the individual reproduces to a certain extent that of the race; but the motionless, imbecile pupa cannot represent a mature form. Fritz Müller considers that the wingless Blattidæ probably most closely represent the original insect stock; Häckel is inclined rather to the Pseudo-Neuroptera. I feel great difficulty in conceiving by what natural process an insect with a suctorial mouth like that of a gnat or butterfly could be developed from a powerfully mandibulate type like the Orthoptera, or even from the Neuroptera. M. Brauer has recently suggested that the interesting genus *Campodea* is, of all known existing forms, that which probably most nearly resembles the parent insect stock. He considers that the grub form of larva is a retrograde type, in which opinion I am unable to concur, though disposed to agree with M. Brauer on the first point. M. Brauer, in coming to this conclusion, relies partly on geological considerations, partly on the fact that larvæ more or less resembling *Campodea* occur among widely different groups of insects. I think there are other considerations which offer considerable support to this view. No one, so far as I know, has yet attempted to explain, in accordance with Mr. Darwin's views, such a life-history as that, for instance, of a butterfly, in which the mouth is first mandibulate and then suctorial. A clue to the difficulty may, I think, be found in the distinction between developmental and adaptive changes, to which I called the attention of the Society in a previous memoir. The larvæ of insects are by no means mere stages in the development of the perfect animal. On the contrary, they are subject to the influence of Natural Selection, and undergo changes which have reference entirely to their own requirements and condition. It is evident, then, that, while the embryonic development of an animal in the egg gives an epitome of its specific history, this is by no means the case with species in which the immature forms have a separate and independent existence. Hence, if an animal when young pursues one mode of life, and lives on one kind of food, and subsequently, either from its own growth in size and strength, or from any change of season, alters its habits or food,

however slightly, it immediately becomes subject to the action of distinct forces: natural selection affects it in two different and, it may be, very distinct manners, gradually leading to differences which may become so great as to involve an intermediate period of change and quiescence.

There are, however, peculiar difficulties in those cases in which, as among the Lepidoptera, the same species is mandibulate as a larva and suctorial as an imago. From this point of view, however, *Campodea* and the Collembola (*Podura*, &c.) are peculiarly interesting. There are among insects three principal types of mouth:—first, the mandibulate; secondly, the suctorial; and, thirdly, that of *Campodea* and the Collembola generally, in which the mandibles and maxillæ are retracted, but, though far from strong, have some freedom of motion, and can be used for biting and chewing soft substances. This type is intermediate between the other two. Assuming that certain representatives of such a type found themselves in circumstances which made a suctorial mouth advantageous, those individuals would be favoured by natural selection in which the mandibles and maxillæ were best calculated to pierce or prick, and their power of lateral motion would tend to fall into abeyance; while, on the other hand, if powerful masticatory jaws were an advantage, the opposite process would take place.

There is yet a third possibility—namely, that during the first portion of life the power of mastication should be an advantage, and during the second that of suction, or *vice versâ*. A certain kind of food might abound at one season and fail at another, might be suitable for the animal at one age and not at another: now in such cases we should have two forces acting successively on each individual, and tending to modify the organization of the mouth in different directions. It will not be denied that the ten thousand variations in the mouth-parts of insects have special reference to the mode of life, and are of some advantage to the species in which they occur. Hence no believer in Natural Selection can doubt the possibility of the three cases above suggested, the last of which seems to explain the possible origin of species which are mandibulate in one period of life and not in another. The change from the one condition to the other would no doubt take place contemporaneously with a change of skin. At such times we know that, even when there is no change of form, the temporary softness of the organs often precludes the

insect from feeding for a time, as, for instance, is the case with the silkworm. When, however, any considerable change was involved, this period of fasting would be prolonged, and would lead to the existence of a third condition, that of the pupa, intermediate between the other two. Since other changes are more conspicuous than those relating to the mouth, we are apt to associate the pupa-state with the acquisition of wings: but the case of the Orthoptera (grasshoppers &c.) is sufficient proof that the development of wings is perfectly compatible with continuous activity; so that in reality the necessity for rest is much more intimately connected with the change in the constitution of the mouth, although in many cases no doubt the result is accompanied by changes in the legs, and in the internal organization. It is, however, obvious that a mouth like that of a beetle could not be modified into a suctorial organ like that of a bug or a gnat, because the intermediate stages would necessarily be injurious. Neither, on the other hand, for the same reasons, could the mouth of the Hemiptera be modified into a mandibulate type like that of the Coleoptera. But in *Campodea* and the Collembola we have a type of animal closely resembling certain larvæ which occur both in the mandibulate and suctorial series of insects, and possessing a mouth neither distinctly mandibulate nor distinctly suctorial, but constituted on a peculiar type capable of modification in either direction by gradual changes without loss of utility.

Before concluding, I must say a few words about the probable nature and origin of the wings. Whence are they derived? why are there normally two pairs? and why are they attached to the meso- and metathorax? These questions are not less difficult than interesting. It seems to me that the wings of insects originally served for aquatic and respiratory purposes. From the various modes by which respiration is effected among the different groups of aquatic insects, we are justified in concluding that the original insect stock was, like *Campodea*, a land-animal. But in aquatic insects there is a tendency to effect the purification of the air through the delicate membranous covering of more or less foliaceous expansions of the skin. In the larva of *Chloëon*, for instance, which singularly resembles *Campodea*, several of the segments are provided with such foliaceous expansions, which, moreover, are in constant agitation, and the muscles of which, in several remarkable points, resemble those of the true wings. It

is true that in *Chloëon* the vibration of the so-called branchiæ is scarcely, if at all, utilized for the purpose of locomotion; the branchiæ are, in fact, placed too far back to act efficiently. The situation, however, of these branchiæ differs in different groups; indeed it seems probable that originally there would be a pair on each segment. In such a case those branchiæ which were situated near the centre of the body, neither too much in front nor too far back, would serve the most efficiently as propellers. The same causes which have determined the position of the legs would affect the wings also. Thus a division of labour would be effected; the branchiæ on the posterior segments of the thorax would be devoted to locomotion, those on the abdomen to respiration. This would tend to increase the development of the thoracic segments, already somewhat enlarged to receive the muscles of the legs.

That wings may be of use to insects under water is proved by the very interesting case of *Polynema natans*, which I discovered in 1862, and which uses its wings to swim with. This, however, is a rare case; and it is possible that the principal use of the wings was, primordially, to enable the mature forms to pass from pond to pond, thus securing fresh habitats and perhaps avoiding in-and-in breeding. If so, the development of wings would tend to be relegated to a late period of life; and by the tendency to the inheritance of characters at corresponding ages, to which Mr. Darwin has called attention*, the development of wings would be associated with the maturity of the insect. Thus the late acquisition of wings in the Insecta generally seems to be itself an indication of their descent from a stock which was at one period aquatic in its habits, and which probably resembled the present larvæ of *Chloëon* in form, but had thoracic as well as abdominal branchiæ.

If these views are correct, the genus *Campodea* must be regarded as a form of remarkable interest, since it is the living representative of a primæval type from which not only the Collembola and Thysanura, but the other great orders of insects have all derived their origin.

---

* Origin of Species, 4th ed. pp. 14 & 97.